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SOMATIC MUTATIONS AND ELYTRAL MOSAICS OF BRUCHUS.

J. K. BREITENBECHER,

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INTRODUCTION.

During the years 1918 to 1920 thirty-one unusual females were discovered in cultures of *Bruchus quadrimaculatus*.* These unusual types were normal insects except that the elytra were of different colors. Such striking differences as these constitute what the geneticists term mosaics, and because they appear in the elytra the author describes them as elytral mosaics. It is a noteworthy fact, proven by the experiments, that these mosaics are not transmitted; it is necessary, therefore, to assume that these peculiar differences must originate in somatic tissue. It will be evident from the experiment, described herein, that these mosaics manifest an order of dominance in agreement with that of mutations. The author, therefore, concludes that these elytral mosaics are caused by somatic mutations.

It is also a noteworthy fact that these mosaics were more abundantly manifested during the period in which the author was investigating the genetics of the first three mutants (red, black, and white) which he had discovered in the progeny of the so-called "four-spotted cowpea-weevil," *Bruchus quadrimaculatus* Fabr. In a previous paper (Breitenbecher, '21) the behavior of these mutants was described and a multiple allelomorph system demonstrated for the factors which involve the four-body and elytral colors as discovered previously for *Bruchus*. Here the author proved that the order of dominance for these four-color factors was red, black, white, and tan (the wild type). The females and males of the wild type have tan elytra and bodies, while the females

* Since this paper was sent to press, 17 new mosaics have been observed, making a total of 48 to date.

of the white mutant cultures have white elytra and bodies and the males have tan elytra but gray bodies. The black mutant stock shows a more pronounced dimorphism, since its females had black elytra and bodies, and its males tan elytra but grayish-black bodies. A lesser difference is seen in the red mutation, for its females had red elytra and bodies, while its males had tan elytra and reddish-gray bodies. It is evident from this description that every male had tan elytra. In conformity with an allelomorph series, the following formulæ were designated by the author: red ($R R$), black ($R^b R^b$), white ($R^w R^w$), and tan or wild ($r r$). These formulæ also indicate the order of dominance.

TABLE I.

THE DATA ON THE ORIGIN, APPEARANCE, AND OFFSPRING OF ELYTRAL MOSAICS IN BRUCHUS.

Mosaic No.	Date Discovered.	Found in a Pure Culture of	Mosaic Female Elytral Color		Bred to a Male Pure for	Offspring Summary.
			Left.	Right.		
1	1918 April 20	Black	Black	Red	Black	None
2	" May 18	"	"	"	"	"
3	" Aug. 18	Wild	Tan	Black	Wild	All wild
4	" Aug. 28	Black	Black	Red	Black	" black
5	" Sept. 21	"	Red	Black	"	None
6	" Sept. 30	Wild	Black	Tan	Wild	All wild
7	" Oct. 7	Black	"	Red	Black	None
8	" Oct. 15	"	"	"	"	All black
9	" Oct. 22	"	"	"	"	" "
10	" Nov. 7	"	"	"	"	" "
11	" Dec. 2	"	"	"	"	" "
12	" Dec. 12	"	Red	Black	"	" "
13	1919 Jan. 2	"	"	"	"	" "
14	" Jan. 5	Wild	Tan	"	Wild	All wild
15	" Jan. 12	Black	Black	Red	Black	" black
16	" Jan. 14	Wild	Tan	Black	Wild	None
17	" Jan. 16	Black	Red	Black	Black	"
18	" Jan. 17	Wild	Tan	"	Wild	"
19	" Jan. 21	Black	Black	Red	Black	All black
20	" Jan. 23	Wild	Tan	Black	Wild	None
21	" Jan. 23	Black	Red	"	Black	None
22	" Jan. 23	Black	Black	Red	"	All black
23	" Jan. 25	"	"	"	"	" "
24	" Jan. 27	"	"	"	"	" "
25	" Jan. 27	"	Red	Black	"	" "
26	" Feb. 12	"	"	"	"	" "
27	" Mar. 27	"	Black	Red	"	" "
28	" Apr. 12	"	Red	Black	"	" "
29	" July 16	Wild	White	Tan	Wild	All wild
30	" Dec. 9	"	Tan	Black	"	None
31	1920 Jan. 1	White	Black	White	White	All white

It is the purpose of this paper to describe the origin and genetic behavior of thirty-one elytral mosaic females which were discovered among thousands of normal insects examined during the progress of this work. The usual expectancy for homozygous cultures is that the elytra of the normal females will be red-red for the red mutant, black-black for the black one, white-white for the white mutant, and tan-tan for the wild type. But for these thirty-one cases, types of mosaic elytra have appeared, such as red-black, black-red, black-white, black-tan, tan-black, and white-tan. It is with these unusual types that this paper is concerned.

TABLE II.

Mosaic No.	F ₁ Elytra Color.		F ₂ Elytra Color.		F ₃ Elytra Color.		F ₄ Elytra Color.		Totals.
	♀ ♀	♂ Tan	♀ ♀	♂ Tan	♀ ♀	♂ Tan	♀ ♀	♂ Tan	
3	3 tan	3	5 tan	20	15 tan	20	21 tan	22	109
4	3 black	3	4 black	6	37 black	41	289 black	351	734
6	2 tan	2	3 tan	3	40 tan	24	120 tan	145	339
8	9 black	7	23 black	31	99 black	87	472 black	462	1,190
9	5 "	8	41 "	45	173 "	163	1,431 "	1,550	3,416
10	13 "	11	76 "	78	201 "	215	2,327 "	2,401	5,322
11	28 "	15	92 "	83	324 "	321	3,213 "	3,337	7,413
12	9 "	10	23 "	29	93 "	101	728 "	719	1,712
13	7 "	3	4 "	1					15
14	4 tan	6	13 tan	18	231 tan	239			511
15	9 black	2	10 black	8					29
19	9 "	19	83 "	91	514 black	565			1,275
22	2 "	2	21 "	28					53
23	8 "	6	139 "	174					324
24	10 "	8	3 "	7					28
25	3 "	4	97 "	93					197
26	42 "	47	317 "	323					729
27	5 "	6	98 "	91					200
28	5 "	8	202 "	224					439
29	15 tan	18	84 tan	89	327 tan	331			864
31	9 white	8	92 white	102	439 white	427			1,077

THE EXPERIMENTS.

The data and results from the breeding experiments which were carried on during the years 1918-1920 are summarized, as they bear upon the question of mosaics, in Tables I. and II. It seems easier to interpret these mosaics if one describes them in the order of their dominance (red, black, white, and tan, or the wild type).

It is evident from consulting Table I. that no mosaic has ever

appeared in any pure culture of red. This fact is significant because red is dominant to black, white, and tan, and if recessive mosaics through mutations occurred in the red stock, they could not be seen. It is of interest to observe that all thirty-one elytral mosaics were females; the reason is, the colors (red, black, and white) are somatically visible in the elytra of this sex, but, on the other hand, no elytral mosaic males were discovered because the elytra of the males of the four types are always tan. Therefore, if a mosaic was produced in a male, it could not be seen, because the characters involved are sex-limited traits.

Twenty-two of these mosaics, described in Table I., originated from homozygous, black cultures. Each of these mosaic females was alike in having a normal black body, except that one elytrum was always red. Of these, eight (Mosaics 5, 12, 13, 17, 21, 25, 26, and 28) had a red, left elytrum and a black, right one, while fourteen (Mosaics 1, 2, 4, 7, 8, 9, 10, 11, 15, 19, 22, 23, 24, and 27) had a black, left elytrum and a red, right one. In order to determine whether a factor mutation had occurred, each of these mosaic insects was mated to a homozygous, black male, and the number of offspring from each pair is given in Table II. The result is the same from every mating; red was not transmitted because all progeny were pure for black. No doubt the fact that red is the only dominant to black explains why the red elytrum was visible. The fact that the black mutant cultures are more prolific and, accordingly, give rise to a greater number of offspring might account for the appearance of more mosaics, unless it is assumed that the mutation from black to red occurs more frequently.

In order to illustrate the red-black, elytral, mosaic type, let us describe Mosaic 12 (Tables I. and II.) as an example. This insect appeared on December 12, 1918, from a pure, black culture. She had a red, left elytrum and a black, right one. She was mated to a pure, black male, because her body color was, likewise, homozygous for black; her progeny were every one pure for the black character. Among the 1,712 offspring no red ones were discovered; however, red was visible in the mother because it is a dominant color to black, which is its recessive allelomorph.

From the fourteen black-red, elytral mosaics let us select Mosaic 9. This animal emerged from a culture which was homozygous

for the black mutation on October 22, 1918. She possessed all the characters which were normal for a black female, except that her right elytrum was red. She was mated to a male with tan elytra, but pure for black, and this pair gave rise to 3,416 pure, black progeny. The same result is evident as before; red was not observed in any offspring, even though they were inbred for four generations; but red was visible, however, in the original parent because it is a dominant color to black.

It is next in order to consider the elytral mosaics which manifested themselves in a pure, white culture. The last mosaic (Mosaic 31, Tables I. and II.) described made its appearance on January 1, 1920, from a culture that was homozygous for the white mutant stock. Her body color and right elytrum were both normal for the white insect, but her left elytrum was black. She was bred to a male normal and pure for white. They produced 1,077 homozygous white descendants. This test indicates the same general behavior relative to dominance. Black is manifested here because it is a dominant color to white. It should be possible also to find among the progeny of a homozygous, white culture both red-white and white-red mosaics, but none were found, because it is almost impossible to keep this stock alive. This is not surprising, since only one mosaic was seen during the progress of this experiment.

Because the tan or wild type is recessive to any of the above body and elytral colors, their mosaics will next be considered. The following dominant mosaics are possible from this type: Tan-white, white-tan; black-tan, tan-black; red-tan, tan-red. Of these possible dominant mosaics three have appeared; the white-tan, tan-black, and black-tan. The others as yet have not occurred.

Thus far only one individual of the white-tan type has been discovered, Mosaic 29 (Tables I. and II.). On July 16, 1919, a remarkable elytral mosaic was found which was different from any of the others. This female had a white, left elytrum and a tan, right one; her body was normal, however, for the wild type. She originated from a wild culture, and when bred to a wild (tan) male produced 864 wild progeny. White was also visible in this elytral mosaic female because white is a somatic dominant color to tan.

This proves that white was not transmitted to any offspring; on the other hand, no tan-white insects have so far appeared.

Another kind of mosaic that was found frequently among the offspring from the wild cultures was an animal with one black elytrum. Six (Mosaics 3, 14, 16, 18, 20, and 30) of these females had tan, left elytra and black, right ones, while one (Mosaic 6) had a black, left elytrum and a tan, right one.

To illustrate the tan-black type, Mosaic 14 will be described. A mosaic female was observed after she had emerged with many other insects from a wild culture on January 5, 1919. This female had a normal, tan body and tan, left elytrum, while her right elytrum was black. When mated with a normal (tan) wild male, her offspring produced through three generations 511 tan or wild descendants. This type of a mosaic proves that black was not transmitted, because it did not appear in any offspring; again black appeared in this insect because black is a dominant to tan, its recessive allelomorph.

Of the black-tan, Mosaic 6 is the only one which was observed. She was found in a culture from wild parents on September 30, 1918. Her body and right elytrum were both tan, but her left elytrum was black. She was mated to a wild male and produced 339 homozygous, wild progeny. The result shows that the black visible in this mosaic was not transmitted because it is a somatic dominant to tan (the wild type).

DISCUSSION.

The result of the experiments previously described shows that these somatic modifications in *Bruchus*, which concern the elytra of the females, are not due to factor mutations in the germ cells, because they are not transmitted. It seems, therefore, that the best interpretation is to assume that they are somatic mutations. Ordinary somatic variations are modifications that are supposed to be caused by environmental factors, as they are not inherited. They always display a normal variability curve. The converse of this is true, for these mosaics, since they manifest a sharp discontinuous variation, not unlike a mutation. Mutations have usually been described as discontinuous variations that breed true. A mutation that occurred in a germ cell in an animal would breed true because

of the necessity of sexual reproduction, but a mutation that took place in a somatic cell could be discontinuous, although it would not be transmitted sexually. This reasoning led the author to suggest that these elytral mosaics in *Bruchus* should be called somatic mutations.

In plants mutations may occur in the germ cells or in any meristematic tissue. According to Babcock and Clausen ('18), "Factor mutations in meristematic cells, or vegetative mutations, as distinguished from those originating in the germ cells, give rise to simple *bud sports* or to *chimeras* according to the location of the mutating cells. A bud sport is a shoot or branch which differs genotypically in one or more characters from the remainder of the plant. Here the factor mutation must occur in one of the undifferentiated cells of the very young shoot. Just as in the case of factor mutations in germ cells, so in vegetative mutations the somatic effects range from single visible character differences to manifold effects in which many structural details are different." The fact that somatic factor mutations do occur in plants seems to be well established, and, furthermore, these somatic factor mutations display the same order of dominance, as manifested by factor mutations, which occur in germ cells. Although somatic factor mutations are extremely rare in animals as compared to this same behavior in plants (because the latter can be propagated, while the former can not be), this, in itself, is not sufficient argument to discredit the idea that the same phenomena are involved. It appears, therefore, in this relation that the mosaics in *Bruchus* are not unlike somatic mutations in plants. Emerson ('21) has lately noted similar phenomena in maize.

The ordinary gynandromorph, as described by Morgan and Bridges ('19), is an animal that shows some male characters on one side of the body and female on the other, but the elytral mosaics in *Bruchus* are not gynandromorphs in this sense because the sexual organs are not modified, every mosaic being a normal female. These authors ('19) further showed that sex-linked characters are usually involved in the gynandromorphs of *Drosophila*. There is evidence that nearly all gynandromorphs are potentially females, but that a sex-mosaic results through the elimination of one sex-chromosome immediately after fertilization; this is due to

the fact that the normal female in *Drosophila* has two (XX) sex-chromosomes in her body, but if one is eliminated on one side of her body, male characters will then develop on that side. There is in *Drosophila* no essential difference between gynandromorphs (sex-mosaics) and somatic mosaics, except that the former concern the elimination of one sex-chromosome, while the latter involve the elimination of an autosome. The mechanism of elimination, too, is the same.

It is true of *Bruchus* that all visible mosaics were females, but the author ('21) has shown that these color factors in this insect are not sex-linked, but are sex-limited, autosomal traits. It is improbable that any change in the X-chromosome could produce these mosaics. Morgan and Bridges ('19) have shown that gynandromorphs are neither caused by partial fertilization, as first suggested by Boveri, nor due to polyspermy, as first interpreted by Morgan, but are caused by chromosome elimination. Chromosome elimination, as described by the above writers, means that during some early stage of development of the embryo one of the daughter sex-chromosomes fails to pass over to the daughter plate, and thereby becomes eliminated from the nucleus. Relative to the mosaics of *Bruchus*, it is impossible to account for their appearance through the elimination of the X-chromosome, because these characters involve the autosome in which the allelomorph series for the R (red) gene is located, and not the X-chromosome.

Morgan and Bridges ('19) account for mosaics of *Drosophila* by chromosomal elimination; in one case they tried to account for the origin of a mosaic, as produced from binucleated eggs, because each paternal nucleus was known to have had a different ancestry. It is unnecessary to make this latter assumption for these mosaics of *Bruchus*, because both nuclei of a binucleated egg (if such could occur) would of necessity be alike, and when fertilized by a normal sperm, all of the offspring would be homozygous, unless it is assumed that a mutation occurred in one nucleus before fertilization, and in that event the effect would not be localized in a single wing, but would involve half the entire body.

In *Drosophila* nearly all mosaics can be interpreted as caused by chromosome elimination, because the homologous chromosome from one parent carries factors that are different from its mate.

If these mosaics of *Bruchus* had originated from heterozygous cultures, then the elimination of one autosome might produce one elytrum of one color and the other of a different one; but since these mosaics came from homozygous cultures, it is evident that the elimination of an autosome previous to or even after fertilization could not have this effect. It is difficult to conceive of any kind of autosomal non-disjunction that could possibly create a red elytrum, for example, when the insect was pure for black. Neither can non-disjunction nor the elimination of an autosome have any effect in causing this kind of a mosaic unless one assumes that a mutation occurs after fertilization. The evidence is in favor of this interpretation because these mosaics are not transmitted. It appears, therefore, more reasonable to assume that a mutation has occurred in one autosome during the embryonic development of the insect. Neither is it necessary to assume that autosome elimination or non-disjunction is essential to account for these mosaics even after a somatic mutation has taken place, unless these mosaics were recessives instead of dominants.

Normally recessive mosaics could not be seen, even though they occurred frequently, because a recessive autosome mutation could not be visible in the F_1 progeny, except through autosome elimination. To illustrate the appearance of such a mosaic, let us suppose in a pure culture for red that a female was found with one black elytrum (black is recessive to red). The normal autosome complex on each side of the body of a homozygous red female would be RR . If a mutation to black would occur in one autosome on her right side (R^b is the formula for black), then her right side would be RR^b , and her left side, normal, RR ; but because red is dominant to black, when heterozygous, she would still appear red unless the autosome carrying R (red) on her right side would be eliminated, then one side would be black and the other red.

The time in the ontogeny at which the mutation occurred would govern the extent of its effects. If it took place at the first cleavages, for instance, the entire half of the body might be affected; but if it took place later at the time when the *anlagen* of the wings are differentiated, then one elytrum would be black and the other red.

It is true, however, for every mosaic so far discovered in

Bruchus that only elytral colors which are dominant to it have been found, so it is essential to apply next the elimination mechanism to the actual mosaics observed in this insect.

The most common mosaic in this beetle is a red elytrum and a black body originating from pure black stock. This condition is accounted for by assuming a mutation to red in one autosome. Let us now suppose in a normal female, homozygous for black, that, previous to the formation of an elytrum, one autosome mutated to red; the autosomes for the normal elytrum, therefore, would be R^bR^b (pure black), while the mosaic elytrum autosomes R^bR (heterozygous for black and red). Since red is dominant to black, the one R on the one side of this insect is sufficient to make this elytrum red; therefore, a mosaic results as was observed for *Bruchus*. (This is true for the thirty-one mosaics found.) Now, let us apply autosomal elimination for this mosaic; if the autosome R^b (black) was eliminated, the proper mosaic would result; but, on the other hand, if the autosome carrying R (red) was eliminated, the insect would not be a mosaic, but a normal, homozygous, black individual.

Again, if the mutation occurred in two autosomes (a very improbable assumption), it could cause the following mosaic from a homozygous, black insect. Supposing the autosomes on the right side of its body are normal, R^bR^b (black right elytrum), but on the left side a mutation to red occurred in each autosome, then the autosomes for its right elytrum would be RR (pure red). This insect would then have a black right elytrum and a red left one; in this case elimination could not change the mosaic.

The first interpretation with reference to dominant autosome mutations appears correct for these mosaics of *Bruchus*. It seems, therefore, that to account for these mosaics autosomal elimination is not essential, unless a mosaic is visible which is recessive to the normal; in that case autosome elimination would be necessary.

The most plausible explanation, then, is to regard these thirty-one dominant, elytral mosaics of *Bruchus* as somatic mutations that originate in an autosome on one side of the body some time during its ontogeny. The results as described in this paper for *Bruchus* agree with Morgan and Bridges ('19) relative to dominant mutations in somatic tissue. "The general evidence from mutations in

Drosophila," to quote these authors, "makes it highly probable that when a mutation occurs it takes place in only one chromosome of the pair. Hence any mutation in somatic tissue, if recessive, would be concealed by the presence of the normal allelomorph in the homologous chromosome." This is the key to the situation for *Bruchus*, since these thirty-one mosaics appear through dominant somatic mutations in one chromosome of the pair.

It is evident that these somatic mutations in *Bruchus* concern the autosome in which the multiple allelomorph gene for R (red) is located. The difference between the factor mutations which the author ('21) discovered for the body and elytral color factors located at the locus, R, in this autosome and its somatic mutations as manifested in these elytral mosaics is that the former are transmitted, while the latter are not.

The evidence further indicates that there is a chromosome continuity between the gene for R (red) in this autosome in the germ cell and this same gene as manifested through the thirty-one mosaics in *Bruchus*. Of these somatic mutations, twenty-two occurred in homozygous black cultures, through a mutation from recessive black to dominant red; only one from a pure white culture, through a mutation from recessive white to dominant black; while eight appeared from wild stock, seven of these mutated from recessive tan to dominant black, and one of these from recessive tan to dominant white.

The most noteworthy result is that germinal mutations and somatic mutations are identical factor mutations, because both originate through a mutation in a chromosome. This paper furnishes evidence in favor of the chromosome hypothesis.

The conditions noted in these unilateral somatic mosaics perhaps suggest that the chromosome mechanism may also be found to account more generally for the bilateral type of body symmetry, at least in certain groups. Conklin has pointed out that while types of cleavage, symmetry, etc., are determined by cytoplasmic influences, this is not at variance with the chromosome doctrine, since the cytoplasm is itself influenced by the nucleus through the large amount of nuclear material which escapes at every mitosis. The investigations regarding cytoplasmic localization and their part in inheritance merely shows "that in early development inherited

characteristics, like material substances, are chiefly derived from the mother." The facts upon which are based the conclusions recently drawn from a study in asymmetry in *Peromyscus* by Sumner and Huestis ('21) are not necessarily contradictory to Conklin's point of view, in spite of their statement that "the chromosome mechanism of heredity . . . is ill-adapted to account for the transmission of definite spatial relationships. . . ." Future evidence bearing upon the question of symmetry will be very welcome.

SUMMARY AND CONCLUSIONS.

1. During the years 1918 to 1920, among the thousands of Bruchid insects examined, thirty-one elytral mosaic females were found in homozygous cultures of the black, white, and tan stocks. The usual expectancy from pure cultures is that the elytra of the normal female will be red-red for the red mutant, black-black for the black one, white-white for the white mutant, and tan-tan for the wild type, but such mosaic types as red-black, black-red, black-white, black-tan, tan-black, and white-tan have appeared from homozygous cultures. These display the same order of dominance as was discovered by the author ('21) for the four body colors (red, black, white, and tan or the wild type).

2. Chromosome elimination of any kind is not essential to account for these mosaics, but a dominant somatic mutation in one chromosome of the pair is the most plausible explanation. The time in the ontogeny at which the mutation occurred would govern the extent of its effects; the earlier that it took place, the greater its effect. It is evident that it did occur at the time when the *anlagen* of the wings were differentiated, otherwise an elytral mosaic would not have appeared.

3. The difference between the factor mutations which the author ('21) discovered for the body and elytral color factors located at the locus R (red), in an autosome and its somatic mutations as manifested in these elytral mosaics, is that the former are transmitted, while the latter are not. There appears to be a somatic continuity, however, between this gene for R (red) in this autosome in the germ cell and this same gene as manifested through its thirty-one somatic mutations.

4. Of these thirty-one somatic mutations, twenty-two occurred through a mutation from homozygous, recessive black to dominant red; one through a mutation from homozygous, recessive white to a dominant black; while eight originated in wild cultures, seven of these mutated from recessive tan to dominant black, and one of these from recessive tan to dominant white.

5. In conclusion, the most noteworthy result is that somatic and germinal mutations are identical in that both are due to mutations originating in a chromosome. The time in ontogeny at which the mutation occurs determines whether it appears as germinal or merely as somatic.

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